



Oaks were the historical foundation genus of the east-central United States



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ABSTRACT

Foundation tree species are dominant and define ecosystems. Because of the historical importance of oaks (*Quercus*) in east-central United States, it was unlikely that oak associates, such as pines (*Pinus*), hickories (*Carya*) and chestnut (*Castanea*), rose to this status. We used 46 historical tree studies or databases (ca. 1620–1900) covering 28 states, 1.7 million trees, and 50% of the area of the eastern United States to examine importance of oaks compared to pines, hickories, and chestnuts. Oak was the most abundant genus, ranging from 40% to 70% of total tree composition at the ecological province scale and generally increasing in dominance from east to west across this area. Pines, hickories, and chestnuts were co-dominant (ratio of oak composition to other genera of <2) in no more than five of 70 ecological subsections and two of 20 ecological sections in east-central United States, and thus by definition, were not foundational. Although other genera may be called foundational because of localized abundance or perceptions resulting from inherited viewpoints, they decline from consideration when compared to overwhelming oak abundance across this spatial extent. The open structure and high-light conditions of oak ecosystems uniquely supported species-rich understories. Loss of oak as a foundation genus has occurred with loss of open forest ecosystems at landscape scales.

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1. Introduction

Foundation species are dominant species that define ecosystems, influence abiotic conditions, and support biological communities (Dayton, 1972; Ellison et al., 2005). Because foundation species comprise the dominant species, they are easy to identify and serve as general indicators of ecosystem properties such as composition (i.e., affiliated species), stand structures (e.g., density, canopy architecture), principal disturbance agents (e.g., fire), and overall disturbance regime. In addition, shared ecological traits of the dominant species are important to ecosystem function (the mass ratio hypothesis; Grime, 1998; Mokany et al., 2008). Conversely, keystone species, as originally defined, are species of high trophic status that have a disproportionately large influence on their ecosystem relative to their abundance (Paine, 1969). Although first defined as predators within food webs, an expanded definition with little consensus (see Davic, 2003) defines keystone species as any species that has a disproportionately large impact on

ecosystems relative to its abundance, regardless of whether the species is a predator (Power et al., 1996). However, in practice, it is difficult to determine disproportionately large impacts that are 'keystone', as many non-dominant species may be critical to some processes, and therefore, to other species (Mills et al., 1993).

Oaks (*Quercus*) appeared to represent the prototypical foundation species (or more exactly, genus) before Euro-American settlement and land use led to rapid change in east-central United States (Fig. 1; Hot Continental Division). Here, oaks dominated for thousands of years through climate change (Prentice et al., 1991; Abrams, 1992; Williams et al., 2004), similar to the dominance by longleaf pine (*Pinus palustris*) in the Southeast and ponderosa pine (*Pinus ponderosa*) in the West. Historical tree surveys show oaks commonly comprised 30%–80% of presettlement forests (Abrams, 2003; Nowacki and Abrams, 2008). Ecosystems formerly dominated by oak often had open woodland structure comprised of large-diameter overstory trees with an open midstory (Nowacki and Abrams, 2008; Arthur et al., 2012; Hanberry et al., 2014). The high-light conditions of these woodlands supported a rich and diverse composition of light-demanding understory and, in turn, associated fauna. With some disagreement (McEwan et al., 2011),

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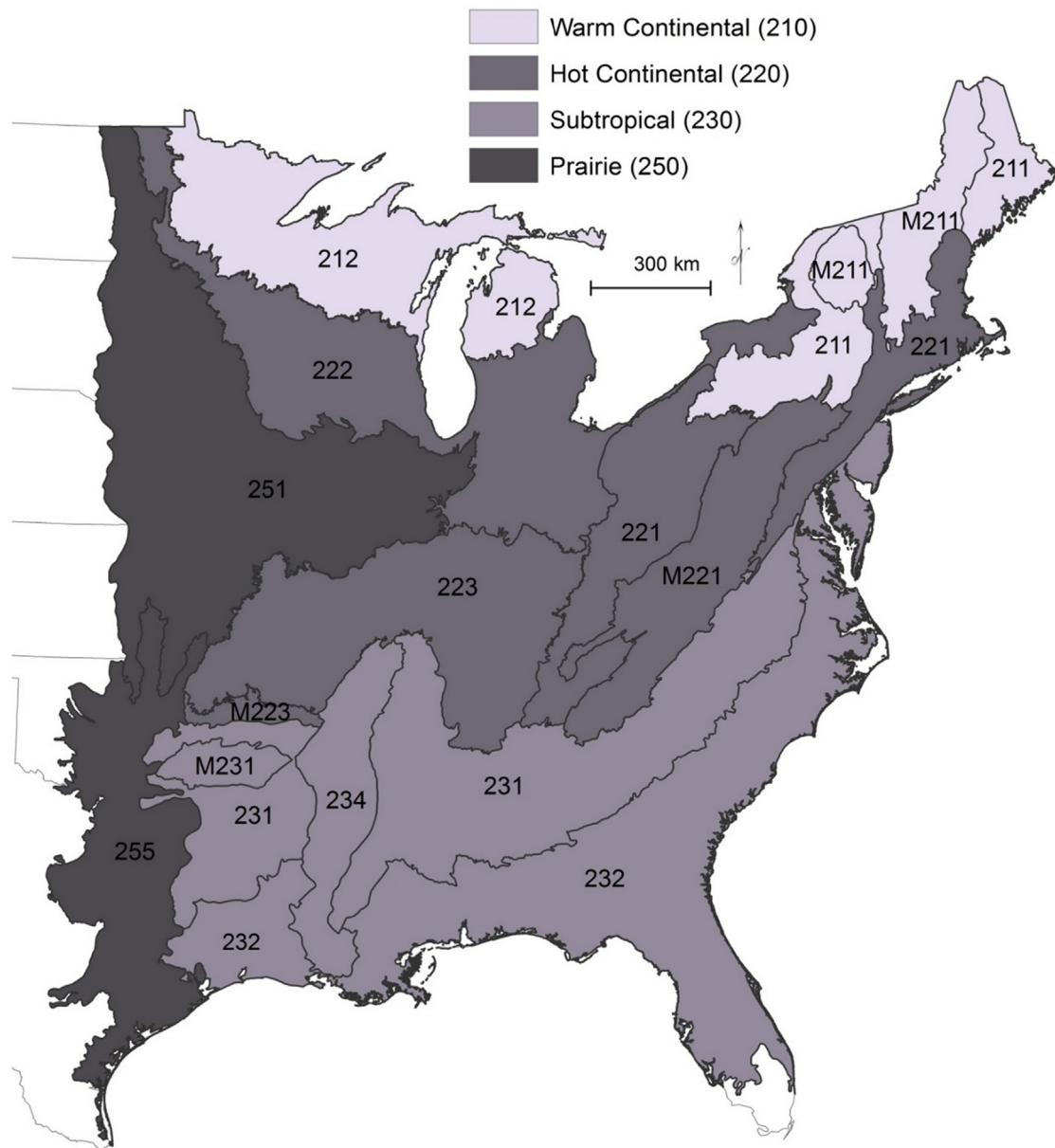


Fig. 1. Ecological divisions (shades) and provinces (alphanumeric codes) of the eastern United States.

the disturbance regime was most likely one of frequent, low-to-mixed severity surface fires that consumed mainly understory fuels and top-killed tree seedlings and saplings, thus reinforcing open stand conditions and fire-tolerant oak and pine species (Hart and Buchanan, 2012; Stambaugh et al., 2015). Across the eastern US, presettlement stand openness increased from east to west concurrent with increasing paleocharcoal and presumably fire frequency and intensity (Patterson and Backman, 1988). Although a great variety of North American oak species exists, 7 oak species historically dominated, usually with membership from both white and black oak subgenera (*Lepidobalanus* and *Erythrobalanus*; Mohler, 1990). White oak (*Quercus alba*) and black oak (*Quercus velutina*) were ubiquitous and formed the core central area, overlapping with northern red oak (*Quercus rubra*) in the north, chestnut oak (*Quercus prinus*) in the east, southern red oak (*Quercus falcata*) and post oak (*Quercus stellata*) in the south, and bur oak (*Quercus macrocarpa*) in the west (Burns and Honkala, 1990; Abrams, 1992, 2003; Hanberry et al., 2012a, c).

In ecosystems where oak was present, co-occurring pines (*Pinus*), hickories (*Carya*), and chestnut (*Castanea*) also were considered common and important structural components in historical landscapes that had a low severity fire regime (e.g., Braun, 1950; Russell, 1987; Ellison et al., 2005; Jacobs et al., 2013). In particular, these genera have been used in common naming conventions (Braun, 1950; Oosting, 1956; Kuchler, 1964; Sanders et al., 1983). However, some care is necessary in the application of terms so as not to reinforce inherited perceptions or 'cultural prisms' (Suffling et al., 2003) based on trees that were highly prized during Euro-American settlement. For example, perception of the importance of iconic eastern white pine (*Pinus strobus*) may have stemmed from its superior timber qualities (Carlton, 1939). Likewise, concerns over red pine (*Pinus resinosa*) may be leading to increased representation (relative to historic levels) in the Great Lakes Region of the US. Specifically, red pine has increased in composition from 1% historically to 10% in southern Wisconsin and from <1% to 4% in southern Minnesota (Hanberry et al., 2013).

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